creek under St. Mawes. The second fishery he mentions took its rise from the quantity of what he calls grampuses and blowers that frequented the coast in the pilchard season; but, owing to mismanagement or some other cause, the concern did not prosper. These grampuses would not have been recognized by naturalists as the species now known by that name, for they seem always to have been rare, and usually solitary in their habits; but they were probably the more common Dolphin. The numbers taken at times at a remote date would seem to show that the ecclesiastical right of the Bishop of Exeter, as mentioned by Anstis, was not unworthy of attention; but it is to be presumed that the merchants of Bayonne were too much alive to their own interests to bring the produce of their fishery within the reach of the bishop's officers, or that of the clerical incumbent of the parish, who made claim to tithe from fish thus caught. Buchanan says, as quoted by Sibbald, that on one occasion—of course, in Scotland—twenty-seven whales were taken as tithes from the number that were caught.

XLIV.—*The Process of Fecundation in the Vegetable Kingdom, and its relation to that in the Animal Kingdom.* By Dr. L. Radlkofer.

[Concluded from p. 365.]

Sect. II. *The Process of Fecundation.*

Our insight into the events occurring in fecundation, into the *essential nature of the process of fecundation,* has been importantly advanced of late, in the *department of zoology* in particular, by direct observation of the behaviour of the spermatozoids in regard to the ovum. Although Keber's* account of the penetration of the spermatozoids into the micropyle of the ovum of the Naiadæ has been shown by Von Hessling's† researches to be fallacious, yet the fact, *that the spermatozoids reach not merely the outer surface of the membrane of the ovum, but, penetrating this, come into direct contact with the vitellus itself,* has been completely demonstrated by the observations of other inquirers.

This was the case first with Barry in the ovum of the Rabbit‡.

* F. Keber, Ueber den Eintritt der Samenzellen in das Ei. Insterburg, 1853.

Ibid. Mikrosk. Unters. üb. Porosität der Körper, nebst ein Abhandl. üb. d. Eintritt der Samenzellen in das Ei. Königsberg, 1854.

† Zeitschr. für wiss. Zoologie, Von Siebold und Kölliker, Bd. v. Heft iv. p. 392 *et seq.*

‡ Martin Barry, Spermatozoa within the Mammif. Ovum. Phil. Trans. London, vol. 133. p. 33, 1843.

His observations were confirmed by Meissner*, and then by Bischoff†, previously Barry's opponent. Beyond this, by Nelson‡ (and Meissner, *loc. cit.*) in *Ascaris mystax*; by Newport§ in the ovum of the Frogs; by Leuckart‖ and Meissner (*l. c.*) in the Insecta; by the latter, also, in *Lumbricus* (*l. c.*); and by Lacaze-Duthiers¶ in *Dentalium*.

The modes in which the penetration of the spermatozoids is rendered possible, are diversified. Either the coat of the ovum (chorion) or vitelline membrane, or both, presents ready-made holes—*micropyles*—at determinate points, especially in those cases where the whole coat is of tough texture (as in the Insecta, in *Gammarus*, in the Holothuriadæ, certain Star-fishes, Worms, bivalve Mollusks; probably also in the Frogs, bony Fishes, &c.); or the coat is of such consistence that the spermatozoids can penetrate at any point whatever, without the pre-existence of orifices, as in the Mammalia**; in a third case, finally, the coat is entirely wanting at the time of fecundation, the ovum consisting then solely of a compact mass of yelk, into which directly penetrate all or part of the spermatozoids, as in the Earth-worm††. We perceive at once, from the last circumstance, that the membrane of the ovum cannot constitute any essential part of the ovum.

Of the subsequent fate of the spermatozoids which penetrate the ovum, of the share which they take in the immediately succeeding changes in the ovum, we must own ourselves, in point of fact, ignorant.

Let us hear Leuckart on this point‡‡: "The only thing that we know definitely is this: that the spermatozoids, which partly penetrate into the vitellus, partly remain in the immediate vicinity of the vitellus, between this and the vitelline membrane, are gradually dissolved (according to my observations on *Melophagus* and *Ephemera*) far more rapidly than spermatozoids which remain outside.....What, however, becomes of the remains of these fecundating elements, is at present unknown to us. .....

* G. Meissner, Beobacht. üb. das Eindring. der Samenelemente in den Dotter. Siebold u. Kölliker's Zeitschr. für wiss. Zoologie, Bd. vi. Heft ii. (1854).

† Bestätigung der von Dr. Newport bei den Batrachien u. Dr. Barry bei den Kaninchen behaupt. Eindring. &c. 1854.

‡ H. Nelson, Reproduction of *Ascaris mystax*. Phil. Trans. London, vol. 142. p. 563, 1852.

§ G. Newport, On the Impregnation of the Ovum in the Amphibia. Phil. Trans. London, vol. 143. p. 233, 1853.

‖ Müller's Archiv, 1855, p. 90 *et seq.*

¶ *Vide* Leuckart, *op. cit.* p. 249.

** Leuckart, *l. c.*

†† Meissner, *l. c.*

‡‡ *Op. cit.* p. 252.

It is extremely probable that the mass of the corpuscles becomes, after solution, mixed with the vitellus, but whether as fluid, or in the form of molecules, we know not; we do not even know whether this mixture takes place only after the completion of the fecundation, or whether it constitutes some essential element of the processes of fecundation and development. Still less, of course, can we judge whether, in the last case, any remnants of the spermatozoids take a direct part in any way in the formation of the embryonal cells, or in the evolution of the embryo."

The former of the two cases here referred to is in favour of the hitherto current theory as to the essential nature of the fecundating process, in accordance with which the spermatozoids perform merely the part of a ferment. Meissner* declares decidedly for the latter. He thinks we may imagine that the changing spermatic elements, like fermenting bodies, may excite in the vitellus, with which, as we now know, they come into direct contact, movements—the immediately commencing phænomena of development—and that at the same time their component parts, which remain in the ovum, do not undergo changes independently of the vitellus, but become at last blended with the parts of this (into an embryonal yelk, as Nelson called it), and constitute a material portion of that which becomes developed into the embryo; he regards the process of fecundation neither as a simple chemical process, nor as a simple contact-action, but as a process *sui generis*, which exhibits traces of the presence of both, but yet is itself neither one nor the other.

Obscure as are at present our conceptions therefore as to the essential nature of the process of fecundation, yet the existing observations appear to me to give satisfactory evidence of two things: first, of the error of Burmeister†, when he regarded "the *male molecular element* (spermatozoid) no longer as merely constituting the vivifying agent in fecundation, but even as the actual *primitive germ*, the primary rudiment of the new organism," and considered "the female individual really as the *alma mater*, which rears, nourishes, and developes the germ delivered to her as a formally and materially determinate rudiment,"—an error which Schacht‡ has also adopted, on which account alone I of course come to speak of it here. From other quarters, besides those above cited, facts come to oppose this hypothesis: the independent, if not ordinarily very far-extended expression of the developmental force which has its seat in the ovum, the segmentation and formal development of embryos in unfecun-

* Siebold u. Kölliker's Zeitschr. f. wiss. Zoologie, Bd. vi. Heft ii. p. 259 *et seq.*, 1854.

† Abhandl. Nat. Ges. zu Halle. 2 Bd. 3 Quartal. pp. 189, 190.

‡ Ueb. Befrucht. der *Pedicularis sylvat.* Flora, 1855, p. 471.

dated ova*. In the second place, it seems to me a settled fact, that the part played by the spermatozoid after penetration into the ovum in fecundation, whether it be a ferment or anything else, is not connected with its *shape*, but purely with the *substance* of which it is composed, and consequently that we need not particularly wonder, if we should meet anywhere in nature with a fecundating substance—I might say spermatozoids —without definite, independent form.

From each vitellus is produced first of all an *individual being* (the embryonal vitellus itself appears to a certain extent as such†). It either remains as such until at the highest stage of its development it has acquired the power of sexual reproduction, or it *becomes multiplied before that epoch by asexual propagation* (by formation of gonidia and buds, division). *A special form of this asexual propagation*, in which the progeny, either of the first or of a subsequent generation, appear *from their origin* onward‡ under a form unlike that of the asexual plant—as *nurses*—is known by the name of *alternation of generations*§. This is a

* Leuckart, Article 'Zeugung,' in Wagner's Handwörterbuch der Physiol. Bd. iv. p. 958 (1853). I shall not refer here to the observations of development of individuals from unfecundated ova of *Daphnia*, *Talæporia*, *Psyche*, &c., the explanation of which is perhaps still to be discovered. But, as will be seen clearly in the sequel, the clothing of the unfecundated spore of *Fucus* by a cellulose membrane, and the formation of tubular prolongations from these, is certainly connected with the above questions. (Thuret, Ann. des Sc. nat. 4 sér. ii. p. 204, 1854.)

† I consider myself quite justified in leaving unnoticed, as insufficiently established, the single case, as yet contradictory of the above, of the occurrence of several embryos in one ovum in *Planaria*. The accounts given by Van Beneden of a subdivision of originally simple ova of *Tubularia* and *Hydractinia* into several smaller ova, each of which produces an embryo, are, as Prof. Gegenbaur of Jena informs me, already refuted; and also those of Koren and Danielssen, forming a counterpart to the former, as to a supposed fusion of every 20–40 of the fecundated ova of the Gasteropodous genera *Buccinum* and *Purpura* into a common mass, which produced only one single embryo. [See on this point Ann. Nat. Hist. ser. 2. xix. pp. 336, 433, and xx. p. 6.—A. H.]

‡ Following Leuckart, we do not include in the conception of *alternation of generations* the case certainly not yet discovered in the Animal Kingdom, but conceivable, and actually occurring in the Vegetable Kingdom—in the propagation of Algæ by zoospores, which again multiply before their metamorphosis into the plant, unless we rather regard them as gonidia, and therefore as larvæ,—where an undeveloped animal (larva) should produce by asexual generation a multitude of individuals like itself, which, no matter whether in the first or a later generation, would become capable of going through the metamorphosis not completed by the latter, in which case, consequently, the metamorphosis would appear, not as associated with reproduction, but merely as a transformation of a being;—this we regard as an ordinary metamorphosis with multiple larva-generations.

§ See Leuckart, Siebold u. Kölliker's Zeitschr. Bd. iii. p. 170 (1851), and Article 'Zeugung,' *l. c. supra.*

result of a 'setting-back' (*zurück-greifen*) to a very early stage of development, of the asexual multiplication, which otherwise mostly occurs only just before puberty, and then with variability as to whether the puberty is subsequently attained or not,—or after that epoch*. These themselves are not repeated (at least not in the last generation), but others, *ab origine* different, are produced—the asexual multiplication appears *directly* combined with metamorphosis. Such is the case in Animals.

In the Vegetable Kingdom, the observations of Pringsheim, Cohn, and Thuret on certain Algæ, which are reported with some confirmations in former pages (352–8), have *demonstrated a process of fecundation* exactly resembling that of animals, completed through immediate contact of spontaneously moving spermatic (fecundating) corpuscles with a naked mass of germinal substance† corresponding with the naked vitellus of the Worms. Without contact with the former, the latter remains undeveloped, or its development does not go on beyond the first step (commencement of germination of the spore of *Fucus*‡); the contact, on the contrary, is followed by development, and either proceeds without interruption, or, after definite periods of rest, with or without intermediate forms (intermediate generations), onward to the repetition of the sexual mother-plant.

In the Mosses and Ferns (in the extended sense) we are acquainted, in the spermatic filaments, with structures corresponding exactly to the fecundating corpuscles of the Algæ; here also the germinal vesicle (the daughter-cell of the central cell of the archegonium) is completely analogous to the germinal substance of the above: it requires for its further development the influence of the spermatozoids, whose approximation to it has been observed by Suminski, Mercklin, and Hofmeister (see pp. 348, 352). It may for the present remain as undecided here, whether the germinal vesicle about to be fecundated is, as Pringsheim conjectures, a naked primordial cell, or, as Hofmeister states, already possesses a cellulose membrane. The latter condition, which would correspond to an ovum possessing a vitelline membrane at the epoch of fecundation, would merely require that the spermatozoids, to come into direct contact with the proper vitelline (germinal substance) mass, should penetrate the enve-

* In the case of *Alcyonella*, to be mentioned presently, we see it set back to the rudimentary embryo.

† Cell-contents without coating membrane; "the contents enclosed by this envelope (cellulose membrane) are the essential and original part of the cell, indeed must be considered as the cell even before the enveloping membrane is formed," says Alex. Braun ('Verjüngung,' p. 166); and in this sense I use, in the sequel, the expression 'primordial cell,' without at all including in the conception the presence of a primordial utricle.

‡ Ann. des Sc. nat. 4 sér. ii. p. 204 (1854).

loping membrane. That we are still in some uncertainty on this point, appears scarcely more than a gap in our knowledge; the recognition of the phænomena known to us as a *process of fecundation perfectly corresponding to that of animals,* can no longer be delayed by this.

The fecundating corpuscles of the plants as yet referred to, possess a peculiar, as we usually say, independent motion, like the spermatozoa of most animals. Of most? Even in animals this is not a universal property of the fecundating corpuscles. It is absent in the Isopoda and Amphipoda. Its absence will not therefore deter us, in plants, from acknowledging as fecundating corpuscles, things, which on other important grounds we are obliged to accept as such. We find ourselves in this position in reference to the corpuscles contained in the antheridial cells of the Florideæ. Yet at present we can scarcely venture more than conjectures as to the fecundating process of these plants; we are still in uncertainty which of the parts capable of being regarded as ova, really have that import.

In the Charæ, also, in which we are acquainted with motile spermatozoids, it remains for future researches to furnish evidence of the conjecture ventured on in an earlier page, that the young (primordial?) spore-cell has the import of an ovum.

Neither the independent movement, therefore, of the spermatozoids, nor, as we have already noticed above, their independent form, appear to be essential properties in reference to their final destination—the fecundation of the ovum. They appear only essential to this in ensuring that the fecundating substance, the substance of which the spermatozoids is composed, *arrives at the place of its destination**. Consequently we have no need to be surprised if Nature, where (to speak anthropomorphically) she can accomplish this object in a different way, does not in the first instance organize the fecundating substance into the form of spermatozoids. We meet with this case in the Phanerogamia.

By my researches I have established with scientific *certainty,* that the embryo of the Phanerogamia is produced, not from the end of the pollen-tube, but from a cell—the germinal vesicle—existing in the embryo-sac before the pollen-tube arrives at the latter. Further, it is the general rule, that this remains undeveloped when it does not receive the influence of the pollen-tube†. The fact that no one has happened to think that the

* We are at present ignorant of the arrangement by which this is effected in the animals with motionless spermatozoa.

† In recent years little faith was any longer placed (Mohl, 'Vegetable Cell,' 1851) in the assertions frequently made by the older authors, of exceptions to this rule, in *Cannabis sativa*, *Spinacia*, and *Mercurialis* (*vide* Bernhardi, Sur la Formation des Graines sans l'aide de Fécondation. Ann.

influence of the pollen-tube resides in its *membrane*, is no proof that such is not the case; but it is a sufficient reason for our not introducing such a speculation here. We have not only a right to assume the *transfer of its contents into the germinal vesicle* in those cases where a direct contact of the pollen-tube with the latter takes place, or only the membrane of the embryo-sac intervenes, but we are compelled to assume it in the case where, as the optical conditions alone suffice to show, the contents on the two sides are different.

des Sc. nat. 2 sér. xii. p. 362 (1839), translated from Allgemeine Gartenzeitung, 1839, nos. 41 & 42; also Meyen's Report on an Observation by Ramisch in Wiegmann's Archiv, 5 Jahr. B. ii. p. 42. Berlin, 1839). The more enigmatical therefore appeared the uncontested fact of the formation of seeds and embryos in the introduced female specimen of *Cœlebogyne ilicifolia* (Euphorbiaceæ) without the presence of anthers. (Smith, Linn. Trans. xviii. p. 509. London, 1841.)

To the kindness of Sir William and of Dr. J. D. Hooker I am indebted for materials for the investigation of this phænomenon. *Cœlebogyne*, the male spiked blossom of which is known in Europe only in the Hookerian Herbarium, is cultivated at Kew in company with a great number of other Euphorbiaceæ. The possibility of hybridation was therefore considerable. But this conjecture was necessarily greatly weakened by the observation, that plants of the third and fourth generations still exactly resembled the mother-plant. The circumstance that I detected a dry pollen-grain upon the stigma of one of the fertile germina which I examined, cannot, from its isolated occurrence, counterbalance the evidence against hybridation arising from the permanence of character. I could not discover a pollen-tube in any part of an ovary or ovule of *Cœlebogyne*; in other Euphorbiaceæ selected for comparative examination, there was no difficulty in demonstrating a fragment of a pollen-tube protruding from the mamilla nuclei. The young ovule of *Cœlebogyne* exhibited three germinal vesicles adherent to the internal surface of its upper end; in older ovaries, sometimes one, sometimes two, sometimes even all three, had been converted into embryos. The various conditions of development of the germinal vesicle into the embryo exactly resembled those in all other Euphorbiaceæ.

Naudin has published an account of repeated and fully established observations on the related cases in *Mercurialis annua*, *Bryonia dioica*, *Cannabis sativa*, &c. (Bulletin de la Société Botanique de France, xii. p. 754 (no. 11, 1855), and more at length in the Comptes Rendus of the present year). Liebmann also (Ann. Nat. Hist. 2 ser. vi. p. 395, 1850) reports the formation of an embryo in a Cycad without the influence of pollen. We may mention, finally, Gasparini's account (Note sur l'Origine de l'Embryon. Ann. des Sc. nat. 3 sér. v. 1846, p. 306) of the formation of embryos in Figs developed in summer, which are said never to contain male flowers—although, from the actual words of this writer in a later publication (Nouv. Recherch. sur l'Anat. et la Physiol. du Figuier. Ann. des Sc. nat. 3 sér. xi. pp. 369, 371, 1849), it appears to follow that he detected a pollen-tube in the micropyle-canal of the ovule of the Fig, but mistook its nature.

The cases in the Animal Kingdom comparable with these (*Daphnia*, &c.) have already been mentioned, and we may direct attention on this head to Siebold's recent essay on 'Parthenogenesis.'—Author's Note, Oct. 1856. [See 'Annals,' the present volume, p. 204.—A. H.]

In the case where the point of attachment of the end of the pollen-tube on the outside of the embryo-sac corresponds, not to the point of attachment on the inside of the wall of a germinal vesicle developed into a suspensor, but to the point of attachment of a destroyed germinal vesicle—it can scarcely be decided whether the transit of the contents of the pollen-tube into the former is effected through the intermediation of the latter, or through an exudation of the contents of the pollen-tube over the embryo-sac, which can be shown to occur to a certain extent.

When one sees how the germinal vesicle lying immediately opposite the end of the pollen-tube, the contents of which assume exactly the optical character of the contents of the pollen-tube, is aborted in certain plants with apparently unexceptional regularity, while the other, seemingly less favourably situated, is developed, the idea is not far-fetched, that the further development of the former is arrested actually by the transfer to it of too large a quantity of the dense fluid contents of the pollen-tube. At present we are, indeed, ignorant of the more intimate relations in which the growth or re-formation of a cell-membrane stands to the character of the cell-contents; yet we may assume that both (putting all else out of the question) may be rendered impossible by too slight or by too great a concentration of the formative fluid. It might even be supposed that the contents of the pollen-tube must here first undergo dilution in the one germinal vesicle, to enable it to fertilize the other! Strange as this arrangement may appear to our existing notions, yet, even if a perfect analogy ought scarcely to be sought beyond the limits of the vegetable kingdom, a phænomenon may be referred to which admits of the supposition, that in the fecundation of the animal ovum, also, it may be by no means left to accident how much of the fecundating substance mingles with the vitellus. When we observe, namely, in the ova of the frog, which come in contact on all sides with a great quantity of spermatozoids, that the vitelline membrane is only penetrable by them at a definite and limited spot, while no great resisting power can be attributed to this on physical grounds, it may be admissible to allow the above idea a place in the discussion of this question.

Lastly, by what means the mixture of the *fecundating substance* with that *to be fecundated* takes place in the case where the end of the pollen-tube touches the embryo sac at a distance from the points of attachment of the germinal vesicles, and therefore does not come in contact with any of them, as strangely happens in various plants, according to Hofmeister's recent investigations, which I believe are not yet published*,—by what

[* Hofmeister, Embryo-bildung der Phanerogamen. Jahrb. für wiss. Botanik, i. p. 180. Berlin, 1857.—A. H.]

means this takes place, cannot be quite perceived, unless we assume that such a dilution of the contents of the pollen-tube as must occur here before it can reach a germinal vesicle, does not remove its fecundating properties, or is perhaps even actually necessary for their operation. Such cases alone may yet leave some hope for those who, *in contradiction to the negative results of all existing observations,* still expect, from analogical reasoning alone, *to find morphological fecundating elements—spermatozoids*—in the Phanerogamia.

In the foregoing we have discussed only an endosmotic transit of the contents of the pollen-tube into the embryo-sac and germinal vesicles. Earlier observers, as Meyen* and Cobbold†, and also, quite recently, Henfrey‡, have been inclined to assume that a *copulation* or *conjugation,* analogous to that of the Confervæ, takes place between the end of the pollen-tube and the embryo-sac, thus furnishing a *direct passage for the transit* of the contents of the pollen-tube. We are certainly not of opinion that such a condition is impossible, but must at the same time own that we have never yet been able actually to observe anything of the kind. If such negative observations have but a very inferior value, yet on the other side there exist no positive proofs; and, in addition to this, the circumstance, that in the ordinarily occurring condition of the germinal vesicle to be fecundated, standing at a distance from the end of the pollen-tube, such an arrangement *would not cause a direct passage of the fecundating substance to the mass of germinal substance*—is by no means calculated to render us more inclined to adopt the hypothesis in question.

However this may be, so much is ascertained,—that the contents of the pollen-tube form the analogue of the spermatozoids, the germinal vesicle that of the ovum; *that the fecundating process of the Phanerogamia corresponds completely to that of the Cryptogamia, and to that of Animals.*

Are we justified in distinguishing in the germinal vesicle of the Phanerogamia contents and membrane, like the vitellus and its membrane? It might almost appear so, since we see that in no case does the original membrane of the germinal vesicle take part in the *structure of the embryo itself.* Yet, since the mode of formation of the latter is so different from that of the animal embryo, it may be going too far to try to find analogies here.

It remains only for us to estimate the import of the *conjugation of the Algæ.* Areschoug's observations have removed every difficulty that might have prevented us from regarding it as *a true process of fecundation.* If some room still remain for doubt

* Pflanzenphysiologie, iii. p. 314. † *L. c. supra.*
‡ *L. c. supra.*

whether the contents of each of the conjugating cells are converted into separate cells before copulation, by the formation of an investing membrane, and whether this opinion may not have originated perhaps merely from cases of monstrous spore-formation, similar to those represented by Cohn, fig. 10. pl. 17, in the 'Nova Acta Acad. C. L. C.' vol. xxiv.,—the observations of Areschoug have assured us that the resting-spore originates *only* by the *union* of two masses of plasma developed and nourished in separate organs. We can no longer hesitate to consider one of them as the analogue of the male semen, the other as the analogue of the ovum*. We meet here with a second example of *fecundation without definitely formed spermatic elements.* At the same time we see here unequivocally, the fecundating substance take a direct share in the constitution of the germ (the resting-spore). This simplest case of the fecundating process is that in which its essential nature is most clearly announced.

We also obtain here some important indications as to the proper *signification* of the process of fecundation. For when we behold in the Desmidiaceæ that from the conjugation of two individuals, which are only capable of this act *once*, in each instance only *one* spore is produced, and therefore find the process of fecundation here a *process of reduction* instead of a process of multiplication, we are necessarily led to the conclusion that we must not conceive fecundation to be essentially a means for the multiplication of individuals, *that is, for the maintenance of the existence of the species,* even in those cases where nature has assigned this part to it on account of the complicated organization of a being having rendered impossible a multiplication through direct individualization of one of its parts—that is, through asexual propagation. When we see, on the other hand, how, in asexual propagation, the progeny depart more and more from the type of the first, sexual stock (the ancestors), while this type is restored by sexual reproduction, we can hardly be in error if we regard the fecundating process as essentially the means which nature employs *to maintain the species in its full integrity, corresponding to the original plan of structure.* This object (if, for convenience, we may be allowed so to express it) seems to be so important to it, that in certain cases an effort is made to attain it even at the cost of diminishing the number of individuals. Perhaps this condition is most strikingly exemplified in the behaviour of *Palmoglœa,* in which we see even two individuals, not merely their parts, become blended together, in

* We have already become acquainted with a spore-formation through conjugation in the Fungi also. Unless the position of the plant in question among the Fungi be doubtful, this would be the first case of a sexual reproduction in the class.

order to form the foundation of a series of individuals produced from the conjugated structure by asexual multiplication*. The Protozoa exhibit to us an exactly similar condition in the Animal Kingdom†.

Sect. III. *The different Phases of Development in the Vegetable Kingdom.*

Having recognized the act of fecundation as a universally equivalent formative process, in the majority of the divisions of the Vegetable Kingdom (excepting, namely, the Fungi and Lichens), and as corresponding to the act of fecundation in the Animal Kingdom, we may consider ourselves justified in inquiring how far the stages of development preceding and succeeding this act correspond in various places, and how far the organs most intimately concerned in it stand parallel to each other in physiological and, to some extent, in morphological respects. We do not, indeed, propose to give a detailed exposition of this plan, but must confine ourselves in general to giving merely indications, especially in those cases where the matter seems to declare itself immediately as a result of the facts given above, and entering upon minute discussion only in reference to the more important points. Where gaps occur in the text, the tabular surveys will conveniently complete it, and we therefore refer the reader to them (pp. 457, 458, 459).

In the Vegetable Kingdom, as in the Animal Kingdom, the fecundated germinal mass presents itself as the first rudiment of a new individual being‡. This either remains as such, and sooner or later acquires the capacity to act in the sexual generation of new plants, which course of development we must designate as the highest, in a physiological point of view, of which either plant or animal is capable,—or it *multiplies asexually* before it has attained this stage. *The same form of this asexual multi-*

* Alex. Braun, Verjüngung (Ray Translation, 1851, p. 135).

† Siebold, Zeitschr. f. wiss. Zoologie, iii. p. 62.

‡ I use the term 'individual' only in the ordinary sense, not desiring to enter upon an *exhaustive* definition of it here,—as a single being which presents itself as a living, independent, finite whole,—and this I do on physiological grounds. If, with Alex. Braun, from morphological considerations, we apply the term 'individual' to the shoot, calling, for instance, a tree a colony of polymorphous individuals, a vegetable stock (or phytidom), analogous to the polype-stock or polypidom,—which, however, in a physiological point of view can likewise only be placed beside the simple animal (see Leuckart, Wagner's Handwörterbuch d. Physiol., Article 'Zeugung,' B. iii. p. 975),—the results of the following reflections would be altered in the main only so far that we must assign to the alternation of generations a much more comprehensive field of operation in the Vegetable Kingdom than we are here inclined to do; at the same time we see that phænomenon assume far more complicated conditions. We shall return to this point.

plication which we have called *alternation of generations* in animals, must receive the same name here. The question, whether an alternation of generations, according to the definition which we have above given, is possible in the asexual multiplication *of plants which have attained the highest point of their development* (*puberty*)—a question which we first arrive at here, because no case of this kind is known in the Animal Kingdom—must be answered in the *affirmative*. But this is in such cases of course only possible when the asexually produced progeny, which ordinarily directly repeats the development of its mother, has undergone a retrogressive metamorphosis. We shall refer to this again.

The comparison of *Phanerogamous plants* with animals, as we have attempted it in Table I., scarcely requires discussion. The position of the developed animal as correspondent to the leafy (and rooted) axis, whether this be simple or branched, is a direct consequence of that conception of the individual which we have declared for above. The comparison of the anthers with the testis, of the ovule with the ovary, &c., bears reference of course to morphological conditions.

Very closely connected with the Phanerogamia as most strictly defined, are the *Gymnospermia* (Cycadeæ and Coniferæ), differing from the former only in the internal structure of their ovules, but through this very deviation forming the most direct and easy transition to the groups of *Selaginellæ* and *Rhizocarpeæ*. Hofmeister* has already shown most strikingly that the essential parts of the ovule of the Coniferæ, the secondary embryo-sacs (*corpuscula*, R. Br.), correspond in every respect with those of the archegonia, and, with their neighbouring structures—epithelial appendage, covering-cells,—frequently imitate even the form and structure of the archegonia. The only distinction which can be found between the female organs of reproduction, the essential parts of the female inflorescence of the two groups of plants, is that in the *Gymnospermia* they remain in connexion with the mother-plant until after fecundation is completed, while in the *Selaginellæ* and *Rhizocarpeæ* they separate from it in a very early stage of their development, as rudimentary flowers (megaspores).

If we wish to call to mind further analogies within the reproductive sphere of the two groups, we may mention the behaviour of the pollen-grains on the one hand, and of the antheridial grains (microspores) on the other, in both of which a long interval of time intervenes between the morphological completion and the accomplishment of their functional activity; also the occurrence of a *suspensor* in *Selaginella*.

* Vergleich. Untersuch. p. 140.

Whether or not the suspensor of the Coniferæ, which gives origin to a *number of embryos*, is to be regarded as a *nurse* (Amme), cannot be decided from the varying statements of authors, nor, indeed, until we obtain perfectly continuous series of observations on the stages of development of the Coniferæ. The phænomenon in question would in such case assume a great peculiarity, beyond its early occurrence, from the fact that, since only one of the numerous embryos actually becomes developed,—asexual *multiplication* of a sexually generated individual in truth never taking place,—it would represent little more than an attempt (*sit. ven. verb.*) at alternation of generations.

The antheridial granules of the Selaginellæ and Rhizocarpeæ constitute the most direct transition imaginable between the pollen-grains of the Phanerogamia and the antheridial cells (of an early rank—the mother-cells of the cells producing the spermatozoids) of the Equisetaceæ and the Ferns (in the restricted sense). While they correspond with the former completely in reference to their origin and formation, and even in the earlier features of their subsequent development—the emergence of the internal cell out of the cuticle in the form of a tube,—they agree with the latter in the ultimate formation of definitely shaped fecundating elements inside special vesicles. An immediate approximation to the last process is met with in the pollen-tubes of the Coniferæ, in the occurrence of a distinct cell-formation.

If, led by the unmistakeable analogies which the Coniferæ exhibit, on the one hand with the Phanerogamia, and on the other with the Lycopodiaceæ and Rhizocarpeæ, we have found the right path to the explanation of the import of the fecundating organs in the Ferns (in the wider sense), we shall hardly allow ourselves to be diverted from it again, although in the lower sections of this group, the *Equisetaceæ* and *Ferns proper*, we may find these organs no longer rigidly preserving their original resemblance. We find the germinal vesicle, central cell of the archegonium, and the archegonium itself, here still true to the former type. Only the organ bearing the latter, the female receptacle, the prothallium, undergoes striking metamorphoses. These relate above all to its size, shape, and its relation to the cell (spore) giving origin to it; more remotely they result from the necessities of an independent nutrition (formation of radical fibrils). In the male fecundating organs also we here find diversities connected both with their organization and their position. We have already referred to the former; in regard to the latter, we here no longer find the antheridia connected with the morphologically developed plant, but transplanted, either alone (unisexual flowers), or together with the archegonia (hermaphrodite flower) on to a prothallium. If we understand by the term

flower the totality of the organs necessary for fecundation, or of these together with their immediate support and special envelope when this is present, we may apply the term to the prothallium bearing antheridia and archegonia, as was done by Suminski, the discoverer of the fecundating process of the Ferns; and it may be regarded only as an inessential peculiarity that here this does not attain its perfect development in connexion with the plant which produces it, but separates from the latter in its most rudimentary condition,—we may say, *as the first cell of the flower-bud.*

In the Mosses we find archegonia and antheridia both again developed and their functions completed in connexion with the plant morphologically perfect and arrived at puberty. But from the fertilized germinal vesicle is not produced, as in the Phanerogamia and Ferns (in the widest sense of both terms), an embryo, which—either as primary or secondary axis—grows up, after a period of rest in the former, and immediately in the Ferns, into a plant like the mother; it gives rise to a structure totally dissimilar from the mother-plant, remaining mechanically connected with this, finally, by the production of numerous gonidia (spores) in its interior, which do not give birth to a like progeny, displaying the character of a genuine *nurse* (*Amme*). Its progeny even (of the first generation) do not—in the Mosses, at least—regain the type of the sexual plant; they represent rather a *second generation of nurses—protonema,*—each of which produces a renewed asexual propagation by the formation of buds. It is the individuals originating in this way that assume the power of growing up into sexually-potent plants.

In here agreeing with Henfrey* in regarding the protonema (pro-embryo) of Mosses as a *nurse,* in opposition to Hofmeister's† opinion, I consider it less necessary to justify myself, since in so doing I remain true to the above-given well-established conception of the alternation of generations, than to endeavour to remove the obstacles for those who might find an objection in the difficulty which seems to be produced by the occurrence of a similarly formed pro-embryo in the asexual multiplication of *full-grown* Mosses, on their radical hairs, cells of the leaves, &c. We have discussed above the question whether an alternation of generations is possible in the asexual multiplication of perfectly developed organisms, *i. e.* whether with the asexual multiplication of such can be combined a metamorphosis terminating in the restoration of the mother-type. Such a combination involves, of course, a previous retrogression to a lower stage of development. This is given when the cell of the full-

* Report Brit. Association for 1851, p. 121, note.

† Flora, 1852, p. 6.

grown Moss-plant forms a new protonema-tissue (nurses) in place of immediately reproducing itself; with the asexual multiplication of this is combined the same ascending metamorphosis as before, the propagula of the protonema-threads re-assuming the form of the perfect plant.

The alternation of generations of the Mosses,—both on account of the occurrence of two diverse generations of nurses, and in reference to the production of these, the first time through gonidia*, the second time through buds,—bears a striking resemblance to the alternation of generations in the Trematoda: that the first nurse remains mechanically connected with the mother-plant, seems altogether an inessential condition, and has its counterpart in *Coryne*, in which the sexual animals remain in connexion with the nurse producing them, and almost appear to be the sexual organs (testes and ovaries) of the nurse-individual.

To the much-favoured notion which regards the prothallium of the Ferns as a distinct generation, standing parallel with the leafy Moss-plant (as a sexual generation), while the morphologically developed Fern-plant is placed beside the capsule (with the seta) of the Moss, as a nurse, no objection is to be made, provided the view is carried out logically, and, as is necessary, extended to the Phanerogamia. This carrying-out leads inevitably to a *more morphological conception of the idea of a "vegetable individual,"* in Al. Braun's sense†. We must then regard, not merely the leafy (simple!) Moss-plant bearing antheridia and archegonia, and the prothallium of the Ferns, as well as the prothallium enclosed in the megaspore of the Lycopodiaceæ and Rhizocarpeæ, together with the microspores,—as complete, sexually developed plants, but also the *flowers* of the Phanerogamia, now once and for all corresponding to the prothallium. But if we regard the flower—the floral shoot—as a perfect plant, as an individual, we must attribute the same value to the preceding shoots; we must regard the compound plant‡ as a colony of polymorphous

* These should perhaps be regarded merely as a peculiar form of buds. Montagne described, in a letter to Berkeley (Annals, xvi. p. 354), a monstrosity of *Eucamptodon perichætialis*, the perfectly ripe capsule of which contained buds instead of spores, analogous to the gemmule-cups of *Marchantia*, and Berkeley confirms the fact. In reference also to the import which we have above attributed to the spores of Ferns, Henfrey's remarks on this case appear very much to the point (Ann. Nat. Hist. ser. 2. ix. p. 453, note), when he says that it is a distinct evidence of the *bud-nature of the spores of the higher Cryptogamia.*

† Al. Braun, Das Individuum der Pflanze. Berlin, 1853. (Annals, ser. 2. xv.) See also former note, page 449.

‡ The simple plant, in Schleiden's sense, appears—if, in the present obscurity which prevails upon the laws of the ramification of roots, we may be permitted to regard only the ascending growth—as a colony of homo-

individuals, and the shoots which *necessarily* precede the flower in the series as so many generations of nurses. In like manner with the stems of the Lycopodiaceæ, Rhizocarpeæ, and Equisetaceæ. But then we must not compare the compound Moss-plant as a whole unconditionally with the prothallium (the floral shoot) of the Ferns, but only the floral shoot of the Moss-plant*.

The first two (Lycopodiaceæ and Rhizocarpeæ) would in this case correspond almost completely to the already-mentioned conditions of *Coryne,* since here the developed individuals, at least the males, appear as it were as merely organs appendicular to the nurses. The fact that the assumption of this point of view leads to the appearance sometimes of the nurse (Ferns) and sometimes of the sexual plant (simple Moss) as the *morphologically developed* member of the series,—could not give ground for any limitation of it, since the like occurs in the Animal Kingdom, which, moreover, affords us information that morphological and functional development do not keep side by side in all cases (retrogression of the parasitic Crustacea at the period of puberty).

I hope in this way to have successfully elucidated a contradiction which must have been repugnant to all primary impressions of the facts,—the contradiction which lay in making the prothallium of the Fern equivalent to the ramified Moss-plant, and the separation of the latter from the vegetative formations of all the higher groups of vegetables. Which of the two views I have here attempted to expound, deserves the preference, must be decided by every one for himself, according as he adopts a *physiological* or the pure *morphological* conception of the 'vegetable individual'—until science has decided the point. I confess freely that I have been guided merely by the simple verdict of natural impressions, in for the present inclining to the former.

Against one thing more I must declare, and that decidedly, namely, against the view which makes the Ferns fecundate in the *middle of their lives,* by this becoming capable of growing up to perfection,—according to which, the new individual cycle of development commences not with the *germinal vesicle,* but with the *spore* (in the Mosses as well as the Ferns)†. To show that the name *spore* is applied to *things of very diverse import,* is almost superfluous, after what we have said above‡. The spores of the

morphous (sexual-) individuals, developed without antecedent nurse-formations.

* The merely trifling changes which would thus be required in columns 2nd to the 5th of our Table I. are included in Table II. All the other columns remain unaltered.

† V. Mohl, Vegetable Cell, p. 125. London, 1852.—Al. Braun, Verjüngung, &c. (Ray Translation, 1853, p. 307).

‡ Neither morphology nor the history of development give us invariably

Mosses are gonidia of a nurse; those of the *Ferns* and *Equiseta* correspond to the hermaphrodite or unisexual flower-buds of the Phanerogamia, or rather to the rudiment of these, their primary cell—separating from the mother-plant before their development into flowers; the *megaspores* of the *Lycopodiaceæ* and *Rhizocarpeæ* stand in the same relation to the female flowers of the Coniferæ; the *microspores*, lastly, to the pollen-grains of the Phanerogamia, to which latter may be applied the name 'spores' with the same right as to the previously enumerated structures, since the term can relate to nothing further than individualized cells of similar outward character and corresponding mode of formation, which play a part in the propagation of plants. And yet with so vague a definition we should already take away the name from the spores of the Algæ!

We have already given the reasons for our opinion of the import of the spore of *Chara*. From it, after *a long pause*, directly proceeds a sexually-potent thallus. In this respect it corresponds to the embryo of the Phanerogamia. Its envelope, the sporangium, as Schacht has already rightly observed*, corresponds to the archegonium of the higher Cryptogamia.

The value of the spores and spore-capsules of the *Florideæ* must be decided by future researches.

In the *Fucaceæ* (so far as is known at present) the segmental spore, as primordial cell, corresponds to the unfecundated germinal vesicle of the higher divisions of the Vegetable Kingdom. From it is directly produced the sexual plant.

Among the *Freshwater Algæ*, *Vaucheria* is most allied to the Fucaceæ. A cell preparing germinal substance opens at its apex, and from this moment its membrane becomes a sporangium, and its contents a primordial cell corresponding to a germinal vesicle. After fecundation it presents itself, enclosed by a special membrane, as a completed propagation-cell—embryonal cell, which, after a long rest, is developed directly into the perfect plant.

The fecundation of *Sphæroplea* (and *Achlya*) takes place in a similar manner. The only distinction here consists in the sporangium containing a number of primordial spore-cells, which, as in *Fucus*, are all fecundated!

In *Sphæroplea*, in *Bulbochæte* and *Coleochæte*, the perfect spore presents itself as a *nurse*, whose dissimilar progeny (zoospores) become perfect Algæ. We here meet with retrogression to an asexual multiplication at a very early epoch of life, and it might appear questionable whether we ought to consider the said process merely as such, or as a true *alternation of generations*.

the correct criterion for determining the value of a structure; we must regard the *function* as, above all, decisive on this point.

* Pflanzenzelle, p. 400.

However, the spore-cell, which enlarges and becomes tubular, still remaining simple, before propagation, cannot be considered equivalent to even a very young Alga-thread, and in so far, therefore, the germ-cells (zoospores) asexually produced from it certainly ascend to a higher stage of metamorphosis, since they do not become resting-spores again, but perfect Algæ.

That the form of the alternation of generations is here the same, or nearly the same, as in the asexual multiplication of the developed plant, is certainly a peculiar, yet in our eyes irrelevant condition. When Cohn* sees a resemblance, in the case above mentioned, to the origin of several embryos in the ova of *Planaria*, the well-founded doubt which may be entertained of the correctness of the observation of the latter point is sufficient to make me withhold my assent; besides that I can by no means compare the swarming-spores to an embryo. On the other hand, I believe I have better right to introduce here another case from the Animal Kingdom, as analogous to ours, in which likewise a very early asexual multiplication occurs combined with an immediately advancing metamorphosis,—the case, namely, of *Alcyonella*, whose rudimentary embryo (nurse) gives birth by a kind of gemmation to *two* tufts of polypes†.

In regard to the Algæ *fecundated by conjugation*, I have nothing to add to what I have already said, or to what is indicated in the Tables. Here, also, the perfect spore presents itself as a *nurse*; as in *Palmoglœa*, and probably also in the conjugation-bodies of *Mesocarpus* and *Staurocarpus*, referred to in a former page.

In conclusion, I subjoin a third Table, in which on the one hand the spore, on the other the embryo contained in the seed, are taken as the point of departure of the individual cycle of development, and the separate stages of development placed together in the order of time. The contradictions which occur from this view are too striking for it to be requisite to point them out in detail, and this comparison can only serve to set in a still clearer light the validity of the developments which have been stated in this essay.

[*Note*,—To the Fucoideæ (J. Ag.) furnished with antheridia, mentioned at page 258, should be added, from Thuret's observations, *Tilopteris Mertensii*, Kg. (*Ectocarpus Mertensii*, Ag.) and *Dictyota*. The antheridia and spermatozoids of the latter genus resemble those of the Florideæ (*vide* Thuret, Ann. des Sc. nat. 4 sér. iii. 1855).

To p. 259.—An enumeration of the Florideæ in which the existence of antheridia has been demonstrated is given in the same memoir of Thuret. Al. Braun has also discovered antheridia in *Batrachospermum*, which Thuret includes among the Florideæ (Algar. Unicellul. genera nova, &c. Leipsic, 1855, p. 105).]

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* Entw. u. Fortpflanz. der *Sphæroplea*, p. 16 (Annals, ser. 2. xviii. p. 81).

† See Siebold, Vergleich. Anatomie (1840), p. 33.

TABLE II. (referred to at page 454).

Animal Kingdom.	Mono- and Dicotyledones.	Gymno-spermia.	Lycopodiaceæ and Rhizocarpeæ.	Equiseta and Ferns.	Mosses.
Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.
Embryo.	Embryo.	Embryo.	Embryo.	Embryo.	Rudiment of theca.
Nurse or Nurse-generations*.	Vegetative shoots.	Vegetative shoots.	Vegetative shoots.	Vegetative shoots.	Theca. Protonema and vegetative shoots.
Sexual animal.	Flower-shoot.	Flower-shoot.	Prothallium (and micro-spore complex).	Prothallium (with antheridia and archegonia).	Flower-shoot (bearing antheridia and archegonia).

* These may be absent both in animals and plants; for example, in all plants whose terminal or lateral shoots end in flowers, which therefore present themselves as a nurse-stock, not as a stock of sexual individuals.

TABLE III. (referred to at page 456).

Animal Kingdom.	Phanero-gamia.	Lycopodiaceæ and Rhizocarpeæ.	Equisetaceæ and Ferns.	Mosses.	Algæ.
Embryo.	Seed (embryo).	Megaspore and microspore.	Spore.	Spore.	Spore.
Infancy.	Vegetative sphere (leafy axis).	Prothallium bearing archegonia, and spermatozoids. *Fecundation.*	Prothallium bearing both archegonia and antheridia. *Fecundation.*	Protonema and leafy axis (vegetative sphere).	Thallus.
Puberty. *Fecundation.*	Reproductive sphere (Flower). *Fecundation.*	Vegetative sphere.	Vegetative sphere.	Reproductive sphere (antheridia and archegonia). *Fecundation.*	Antheridia and sporanges. *Fecundation.*
Formation of embryo.	Formation of seed.	Formation of spores.	Formation of spores.	Formation of spores.	Formation of spores.

[The epochs of resting periods are marked (in all the Tables) by blacker lines.]

TABLE I. (referred to at page 450).—*Comparison of the apparently equiva subdivisions of the Vegetable King*

Animal Kingdom.	Phanerogamia.		Pteridoideæ.		Mosses (pr
	Mono- and Dicotyledones.	Gymnosperms.	Selaginellæ, Isoëteæ, and Rhizocarpeæ.	Equisetaceæ and Ferns (*s. s.*).	
Fecundated ovum.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecundated germinal vesicle.	Fecund germi vesicl
Embryo or Nurse.	Embryo.	Embryo.	Embryo.	Embryo.	Theca, S Protone Bud-rudi
Morphologically developed animal.	Leafy axis.	Leafy axis.	Leafy axis.	Leafy axis.	Leafy a
Sexual apparatus.	First cell of the hermaphrodite or each of the unisexual flower-buds.	First cell of the unisexual flower-bud.	Megaspore.	Spore.	Antheri and archego
	Flower: sexes separate or hermaphrodite.	Male and female flowers*.	Microspore—complex, and prothallium.	Prothallium: sexes separate or hermaphrodite.	
Testis.	Anther.	Anther.	Sporangium of microspores.	Antheridia.	Antheri
Spermatic cysts.	Pollen-grain.	Pollen-grain.	Microspore.	Mother-cell of the antheridial cells producing the spermatic vesicles.	Mother-c the anthe cells prod the sperr vesicle
Sperm-cells.	Contents of pollen-tube.	Contents of pollen-tube.	Spermatic vesicles.	Spermatic vesicles.	Sperm vesicle
Spermatozoa.			Spermatozoa.	Spermatozoa.	Spermat
Ovary (and uterus).	Ovule.	Ovule.	Archegonium.	Archegonium.	Archego
Ovarian follicle (Graafian vesicle).	Embryo-sac.	Embryo-sacs, secondary.	Central cell of the archegonium.	Central cell of the archegonium	Central of the ar goniu
Unfecundated ovum.	Unfecundated germinal vesicle.	Unfecundated germinal vesicle.	Unfecundated germinal vesicle.	Unfecundated germinal vesicle.	Unfecun germi vesicl
Germinal vesicle.	Cytoblast of the germinal vesicle.	Cytoblast of the germinal vesicle.	Cytoblast of the germinal vesicle.	Cytoblast of the germinal vesicle.	Cytobla the germ vesicl

* The latter essentially only ovule.

s of Development, Sexual Apparatus, and Sexual Products in the different the Animal Kingdom.

Algæ.						
haræ.	Florideæ.	Fucaceæ.	Vaucheria.	Sphæroplea.	Bulbochæte.	Desmidieæ, Diatomeæ, and Zygnemeæ.
pore. ryonal ell).	Spore?	Fecundated spore.	(Resting-) spore (embryonal cell).	(Resting-) spore (-nurse). Zoospore.	(Resting-) spore (-nurse). Zoospore.	Conjugation-body (resting-spore).
allus.	Thallus.	Thallus.	Thallus.	Thallus.	Thallus.	Thallus.
heridia and rangia.	Antheridia and sporangia? Prothallium?	(Conceptaculum.)	Antheridia and sporangia.	Antheridia and sporangia.	Microgonidia and sporangia.	United conjugation-cells.
heridia.	Antheridia.	Antheridia.	Antheridia.	Antheridia.	Microgonidia and their products in germination.	First conjugation-cell.
ternal s of an- ridium.	Antheridial cellules.					Contents (daughter-cell?) of the above.
leus of rnal cell.						
rmato- zoa.	Antheridium-corpuscles.	Zoospore-like spermatozoids.	Spermatozoids.	Spermatozoids.	Spermatozoids.	
oran- gium.	Sporangium. ??	Sporangium.	Sporangium.	Sporangium.	Sporangium.	Second conjugation-cell.
fecund- d spore- cell.	Unfecundated spore-cell?	Primordial (unfecundated) spore-cell.	Primordial (unfecundated) spore-cell.	Primordial (unfecundated) spore-cell.	Unfecundated spore-cell.	Contents (daughter-cell?) of the above.
		Nucleus of spore-cell.				

† These two intermediate generations absent in the Liverworts.